SELFISH GENEROSITY: COOPERATIVE BREEDING IN BIRDS

by Marta Hersek

For many East Coast birders, spring migration is the highlight of the year — the kettles of migrating raptors, the flocks of brightly-colored warblers passing through, and the occasional lost bird can all be added to our lists. But for those who really enjoy nature-watching, it's what follows that's most exciting; the long spring and summer days are spent watching birds set up territories and settle down for the breeding season. While mating behavior can be endlessly fascinating (Hersek 1997), it's the fruition of all that frantic activity that is really satisfying. Whether you watch a kingbird nest in the backyard, or Ovenbirds nesting in a forest, the drama is never-ending. By carefully observing songbirds, you will see one or both of the birds in each pair build the nest and one or both incubate the eggs; finally, the eggs hatch and nestlings are cared for. You will see that the young are altricial; that is, they hatch at a fairly early developmental stage, blind, mostly naked, and almost completely helpless. They require continual care from the parents for some days: they must be kept warm, since they cannot thermoregulate for the first few days after hatching; they must be fed; and they must be protected from predators.

For most songbirds in New England, this is the typical pattern, with both parents caring for the nestlings and, later, fledglings. There are, however, other systems of breeding and raising young. For example, Red-winged Blackbirds are polygynous; males have multiple mates and nests, so they do not provide care for all of their nestlings. Waterfowl nestlings are precocial (fairly advanced developmentally, and able to walk, thermoregulate, and feed themselves immediately), and often are protected mainly by the female. The system which is the focus of this essay, cooperative breeding, has yet a different twist to it. Cooperative breeding is generally defined as a breeding system in which one or more members of a social group (often referred to as "helpers-at-the-nest") care for offspring that are not their own, but there is great variation with respect to the particulars (Stacey and Koenig 1990). In species like the Florida Scrub-Jay (*Aphelocoma coerulescens*), the social group consists of a monogamous breeding pair plus their mature young from previous years. All group members take part in territory defense and protecting and feeding nestlings (Woolfenden and Fitzpatrick 1990). A more complex system is found in White-fronted Bee-eaters (*Merops bulockoides*). Bee-eaters nest in colonies of 50-300 birds, and each colony consists of smaller extended-family groups called clans. Within each clan there are a number of nesting pairs, each assisted by helpers (Emlen 1990). Finally, Acorn Woodpeckers (*Melanerpes formicivorus*) have a system in which the breeding is not done by one monogamous pair. In this species, groups consist of one to four breeding males, one or two breeding females, and up to eight helpers, who are usually mature offspring from previous years (Koenig and Stacey 1990). There are no obvious pair bonds between individuals, and all breeding females lay in a communal nest. All group members care for the young, as well as take part in defending the territory and storing food. Overall, these cooperative breeding systems are fairly rare. This type of system is currently known to occur in about 220 species of birds.

The reason that cooperative breeding systems are so interesting to biologists, however, is not just that they are rare. The question that puzzles us is, "Why would an individual spend time and energy raising the offspring of another bird, instead of raising its own?" Because we work with the understanding that behaviors like parental care have evolved via the process of natural selection, we assume that a bird's behavior benefits that bird in some way. That is, behaviors evolve which further an individual's survival and/or reproductive success.

In fact there is new evidence that helping behavior by nonbreeding birds has indeed specifically evolved and is not just the result of an adult happening to be around when nestlings are begging, and therefore being stimulated to provide food. Brown and Vleck (1998) looked at two closely related species, the Mexican Jay (*Aphelocoma ultramarina*) and the Western Scrub-Jay (*A. californica*). Mexican Jays have helpers-at-the-nest, while the scrub-jays do not. They found that the hormone prolactin, which is important in stimulating parental behavior, was found at higher levels in the cooperatively breeding Mexican Jay than in the Western Scrub-Jay. Furthermore, the hormone begins to peak in the adults (including the helpers) even before the young of the year hatch. This suggests that the birds have evolved in such a way that they are prepared to care for young, even if they have not been involved in mating or egg-laying, and even if the young are not their own.

We can restate our question, then, and ask, "How does an individual benefit by caring for the offspring of others?" This puzzle is best understood by looking at its two parts. First, why the birds delay their own reproduction, and second, why, even if they don't breed, they assist others.

Delaying Reproduction

In some cases, delaying reproduction simply results from the inability to find a mate. For example, the adult sex ratio is highly male-biased in Pied Kingfishers (*Ceryle rudis*), and first-year males are often unable to breed (Reyer 1987). However, the most common reason that young birds stay in their natal territories and help their parents, rather than breeding on their own, is that they are constrained by a shortage of suitable breeding sites. If breeding is dependent upon having a territory with particular features, as is often the case for birds, and if such territories are not available, then a young bird might best stay in its natal territory and wait for an opening. Although it is difficult to test this hypothesis because it is usually hard for us to determine exactly what constitutes suitable habitat, a convincing case has been made for a number of species. For example, Acorn Woodpeckers are cooperative breeders that also communally store and defend large food stores, called mast. Mast is comprised mainly of acorns, and it is stored in special mast trees that have had many holes pecked into them over years; single individuals are unable to store and defend mast (Koenig and Stacey 1990). This stored food is critical to winter survival and subsequent spring reproduction in much of the species' range, and it is aggressively defended from all who would steal it — including other Acorn Woodpeckers. In these birds, then, survival and reproduction depends upon being part of a group that has a territory and a dependable stored food source. Youngsters that stay in their group's territory apparently monitor nearby groups to watch for a breeding position to open, while remaining relatively safe at home. This is especially important because immigrating to a new territory and social group can be dangerous — entering new areas, often having to fight one's way into a group, and living in marginal habitat in the meantime can all lower a bird's chances of survival.

Assisting Others

Once we understand why young birds may not be able to breed during a particular year, the next question we can ask is why they should assist others. That is, if a young bird stays on its natal territory in order to wait for appropriate breeding positions or territories, why would it spend energy taking care of nestlings that don't belong to it? It may be that the extra birds are "obligated" to help, in order to stay on the territory. This would require the breeders to distinguish between birds that are and are not helping, and to expel the latter from the area. Such aggression toward auxiliary birds has not been observed. In some cases, helping may make it more likely that the individual inherits the breeding territory or position. For example, some young male Pied Kingfishers help unrelated pairs in one year, and return to breed with the female in the next (Reyer 1987). It may be that auxiliary birds are building alliances with others, so that they can emigrate together, when the time is right. In general, however, researchers have focused on two main hypotheses for why nonbreeders help. First, helpers may gain some direct benefit in terms of experience, which later makes them more successful in caring for their own offspring. Second, in accordance with the idea of natural selection, they may actually be passing on their own genes by assisting their parents, by a process called kin selection.

Experience

If birds gain some valuable experience by assisting their parents, then it would make sense to expend the energy to do so while still on the natal territory. There is some evidence that inexperienced birds can learn from helping. For example, adult Long-tailed Tits (*Aegithalos caudatus*) perform helping duties if their own nest fails. Hatchwell et al. (1999) found that nest failure was very high, largely due to predation, and that nests built lower to the ground were more likely to succeed than higher nests. Interestingly, they found that birds that had helped at a successful nest were subsequently more likely to place their own nest lower to the ground, suggesting that they had learned about nest placement by helping a successful pair.

Kin Selection

In 1964, W.D. Hamilton gave us one way to think about behavior that appears to decrease an individual's own reproduction (Hamilton 1964). He recognized that an individual's genetic contribution to future generations can come about in two ways. Most obviously, individuals can pass on their genes through their own descendent kin. But individuals are also genetically related to others – such as their siblings, with whom they share an average of 50 percent of their genes. So if individuals help raise siblings, they are, in effect, passing on their own genes. In cooperative breeding systems, the auxiliary or helper individuals are usually offspring of the breeders, so they are in fact helping to raise nondescendent kin that share their genes. In evolutionary terms, this is as good as passing on your own genes directly. The question of how helpers benefit from their behavior, then, comes down to whether they increase the number of their parents' offspring over what their parents could raise alone — that is, if helpers are gaining some extra genetic benefit from helping. In a number of cases we see that helpers do increase the number of young that breeders raise. For example, a study of White-throated Magpie-jays (*Calocitta formosa*) found that breeding pairs with more helpers were able to renest more frequently, and therefore raise more young, than breeding pairs with fewer helpers (Langen and Vehrencamp 1999). White-fronted Bee-eaters (Emlen 1990), and Galapagos Mockingbirds (*Nesomimus parvulus*; Curry and Grant 1990) both raise more offspring with more helpers.

One final example will make clear just how many factors affect the outcome for helpers. In Pied Kingfishers, a young male that cannot find a mate during his first year as an adult has a number of options (Reyer 1987). Some males become "primary helpers" to their parents. Others help unrelated pairs as "secondary helpers," and still others do not help any nesting pairs. The primary helper works the hardest at his helping duties, and this is reflected in a much lower rate of survival into the next year. Furthermore, primary helpers that survive are less likely to find a mate than secondary helpers, who often mate with the female they helped the previous year. So primary helpers assist their parents at the cost of their ability to reproduce on their own in the future. Calculations of the number of young raised in nests with primary helpers (which, remember, are siblings of the helper) show that these males greatly increase the reproductive success of the parents. Further calculations of the overall genetic contributions of primary and secondary helpers demonstrate that, even with the lowered chances of future reproduction, males that become primary helpers generally have higher success at passing on their genes than other males (Reyer 1987).

Often we see things that do not make sense to us because we're thinking in terms of our own behavior, or in terms of preconceived ideas about how things work. Cooperative breeding systems fell into this category for some years. As is so often the case, careful observation and experimentation have helped us begin to make sense of a system that was at first quite puzzling. In fact, in this case it was really Hamilton's theoretical insight that opened new avenues of thought and allowed us to better understand complex behavior patterns.

Although we have no truly cooperatively breeding birds in New England, we do see interesting examples of helping behavior. For example, House Sparrows (*Passer domesticus*) are frequently observed feeding or otherwise caring for chicks that are not their own (Skutch 1999; Hudson, this issue). These examples are not considered to be cooperative breeding because the birds do not regularly form cohesive social groups, but we can consider them as part of a continuum of possibilities. Why is it that we see certain systems in particular geographic regions, and not in others? Why are cooperative systems more common in the southern and western United States, and in the tropics? Scientists have some thoughts on this matter, which could fill many more pages. For now, next time your travels take you to the far reaches of our country, or into the tropics, spend a little time really watching the birds that you find, and you might be rewarded with some surprises — some behaviors that don't fit your preconceived ideas about how animals "should" behave.

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